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Research Article

Out on a limb: arboreal camera traps as an emerging methodology for inventorying elusive rainforest mammals

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Abstract
Traditionally, arboreal rainforest mammals have been inventoried using ground-based survey techniques. However, given the success of camera traps in detecting secretive terrestrial rainforest mammals, camera trapping could also be a valuable tool for inventorying arboreal species. Here we assess, for the first time, the effectiveness of arboreal camera traps for inventorying arboreal rainforest mammals and compare the results with those from other methodologies. We do so in one of the world's most biodiverse conservation areas, the Manu Biosphere Reserve, Peru. We accumulated 1201 records of 24 arboreal mammal species. Eighteen species were detected by arboreal cameras, seven by diurnal line transects, six by nocturnal transects and eighteen through incidental observations. Six species were only detected using arboreal camera traps. Comparing arboreal camera traps with traditional ground-based techniques suggests camera traps are an effective tool for inventorying arboreal rainforest mammal communities. They also detected more cryptic species compared with other methodologies. Daily detection frequency patterns were found to differ between ground-based techniques and arboreal cameras. A cost-effort analysis indicated that despite greater upfront costs in equipment and training for arboreal camera trapping, when accounting for the additional survey hours required to provide similar numbers of records using ground-based methods, overall costs were similar. Our work demonstrates that arboreal camera trapping is likely to be a powerful technique for inventorying canopy mammals. The method has considerable potential for the study of charismatic and threatened arboreal mammal species that may otherwise remain largely unknown and could quietly disappear from the world's tropical forests.

Keywords: Canopy, habitat disturbance, hunting, threatened species, survey methods.

Resumen

Tradicionalmente, los mamíferos arbóreos de los bosques tropicales, han sido inventariados utilizando técnicas de estudio a nivel terrestre. Sin embargo, dado el éxito de las cámaras trampas en la detección de mamíferos tropicales terrestres con hábitos secretivo, potencialmente evaluaciones con cámaras trampa podrían también proporcionar una herramienta valiosa para el inventario de especies arbóreas. Aquí, por primera vez, evaluamos la eficacia de las cámaras trampa arbórea para el inventariado de mamíferos tropicales arbóreos y los comparamos con los resultados provenientes de otros métodos. Este estudio se realizó en uno de las áreas de conservación con mayor biodiversidad en el mundo, la Reserva de Biosfera de Manu. Se acumularon 1201 registros de 24 especies de mamíferos arbóreos; 18 especies fueron detectados con cámaras trampa arbóreas, siete con transectos diurnos, seis con transectos nocturnos y 18 especies a través de observaciones incidentales. Seis especies fueron detectadas únicamente utilizando cámaras trampa. Comparando las cámaras trampa arbóreas con las técnicas terrestres tradicionales, se sugiere que las cámaras trampa arbóreas son una herramienta eficaz para la detección de la comunidad de mamíferos arbóreos de hábitos secretivos, y que además detectan un mayor número de especies cripticas en comparación con otras métodos. También se encontró que los patrones diarios en la frecuencia de detecciones difirieron entre las técnicas terrestres y de cámaras trampa. Finalmente un análisis de costo-esfuerzo índico que a pesar del gran coste inicial en equipos y capacitación para la evaluación con cámaras trampa, al contabilizar las horas adicionales de muestreo que se necesitarían para proporcionar un número similar de registros usando metodologías terrestres, los costos generales fueron similares. Nuestro trabajo demuestra que las evaluaciones con cámaras trampa arbóreas sean probablemente una técnica poderosa para el inventariado de mamíferos de dosel. La metodología también presenta un potencial considerable para el estudio de especies de mamíferos arbóreos carismáticas y amenazadas que de lo contrario presentan el riego de pasar desconocidos y que tranquilamente podrían desaparecer de los bosques tropicales del mundo.

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Introduction

Rainforest habitats are spatially complex environments [1] that contribute significantly to global biodiversity [1, 2]. Part of this complexity is evident in the vertical stratification of different faunal communities between terrestrial and canopy layers [3-7]. Research suggests that arboreal rainforest mammal species should be high conservation priorities because habitat alteration due to anthropogenic activities causes a greater disruption to arboreal than to terrestrial biodiversity [4, 7-11] and, as with rainforest mammals in general, they are often prey to human disturbance in the form of hunting.

Improving our understanding of arboreal rainforest mammals is crucial as they serve as charismatic flagship species for conservation [12] and are essential ecosystem engineers [13], acting as integral dispersers of fruits and seeds [10, 14] and as key rainforest pollinators [15]. Despite their importance, knowledge of the ecology and distribution of many arboreal rainforest mammals remains sparse due to secretive, cryptic and nocturnal behavior that makes them particularly difficult to survey [12].

Traditionally, medium-large arboreal rainforest mammals have been assessed utilizing ground-based survey techniques, such as line transects, visual searches and acoustic surveys [16-19]. However, attempting to see through dense understory into the upper reaches of 20-40 metre high rainforest canopy is challenging, especially for spotting inconspicuous, cryptic and nocturnal species [20]. For this reason the majority of studies on arboreal rainforest mammals focus on diurnal, vocal, and conspicuous primates which results in incomplete studies of arboreal mammal communities [12]. Additionally, using human observers to address questions relating to hunting pressure can introduce unknown biases regarding the differential degree of human avoidance behaviour between hunting and non-hunting areas [21-24]. Terrestrial camera traps circumvent such issues [20, 25-27], particularly when used for the detection and assessment of elusive, nocturnal and hunted rainforest species [28-33]. Whilst the benefits of terrestrial camera trapping are well documented [26, 28, 32, 33], the potential effectiveness of using camera traps in the canopy to survey arboreal mammals remains largely unknown.

The success stories from terrestrial camera trapping projects suggest that there could be several potential benefits to arboreal camera trapping. First, as arboreal camera traps function 24 hours a day, they have the potential to rapidly inventory arboreal rainforest mammal communities and detect both diurnal and nocturnal species. Second, they can be left for extended periods *in-situ* (potentially for several months) in order to maximize detection opportunities. Third, they have the potential to provide novel ecological information, as behaviors only rarely detectable to human observers can be recorded. Finally, cameras have the potential to provide an unbiased means of assessment within hunted areas, as animals are unlikely to associate cameras with hunters and should therefore be less susceptible to displaying avoidance behavior. Despite these potential benefits, arboreal camera traps have so far only been utilized successfully to study single species behavior [34-37], frugivore feeding preferences [36, 38] and, in one specific case, to document the use of natural crossing points over a gas pipeline clearing [39]. No studies to date have assessed arboreal camera traps for effective inventorying of arboreal mammal communities within typical tropical forest habitats.

This study therefore assessed, for the first time, the effectiveness of arboreal camera traps to inventory medium-large arboreal rainforest mammals. The study took place in one of the world's most biodiverse and important conservation areas, the Manu Biosphere Reserve in Peru, a UNESCO World Heritage Site established to protect the globally important Amazon rainforest and its biodiversity. Specifically the study aimed to: 1) compare arboreal medium-large mammal inventories obtained by classical ground-based approaches with inventories from arboreal camera traps; 2) determine the potential of arboreal camera traps to record species that are difficult to detect (both naturally secretive species and species that might be difficult to detect because of regular hunting by humans); 3) investigate if detection rates varied between cameras located within the lower (8-12m) and upper (18-33m) canopy in order to establish at what heights arboreal camera trapping might be most effective; 4) compare the cost and effort involved in using arboreal camera traps with classical ground-based survey approaches; and 5) assess the potential of arboreal camera traps for obtaining useful or novel ecological information.

Methods

Study Sites

This study was carried out at two sites within the Manu Biosphere Reserve in south-eastern Peru (Fig 1.). The first of these was the Manu Learning Centre (MLC) research station (71°23'28"W 12°47'21"S), which is owned and operated by the Crees Foundation, a conservation NGO. This site is a private reserve comprising of 643ha of regenerating lowland tropical forest covering an altitude range of 450-740m asl. The MLC reserve has a known history of anthropogenic disturbances, ranging from complete clearance for intensive agriculture in some areas, to selective logging for the most commercially valuable timber in others. Regeneration of the forest at the site has been on-going for at least 30 years and, since 2002, the site has been strictly protected from hunting and other human impacts. Biodiversity studies have been ongoing at the site since 2003 and a thorough inventory of many taxa, including amphibians, butterflies, birds, mammals and reptiles, already existed at the time of our study [40]. As such, this site provided an opportunity to assess the arboreal camera trapping methodology in an area with a well-developed species list of arboreal mammals and which was free from the effects of hunting. This was thus the primary site for testing our methodology.

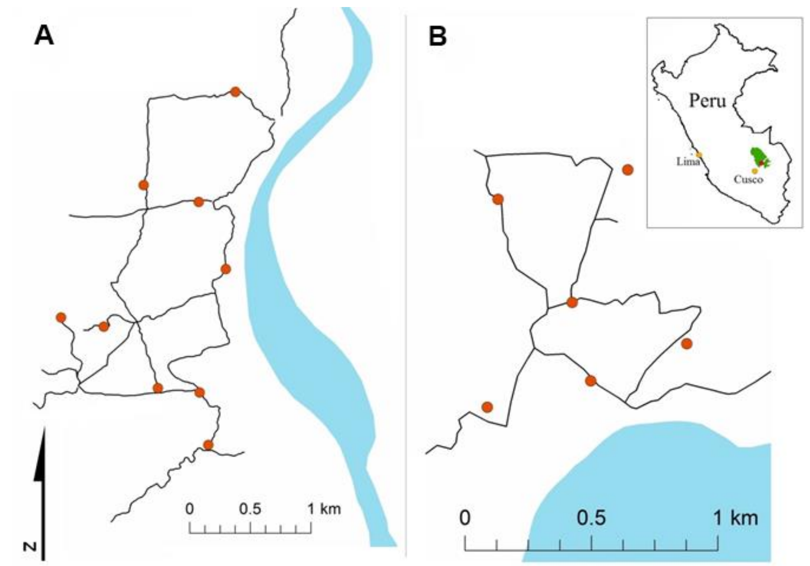

Fig. 1. Study area. The map inlay shows the location of Manu Biosphere Reserve (green) in south-eastern Peru. A) shows the trail system used to survey the Manu Learning Centre Reserve (MLC:~643ha); and B) the trail system to survey Shipetiari (~252ha). Red circles indicate arboreal camera trap survey locations.

In order to examine whether arboreal cameras would still be effective in a different context, we also tested the methodology at a secondary site that was subject to ongoing human disturbance in the form of hunting. This was an area of some 26,800ha (71°9'59"W 12°28’60"S) owned by the Native Community of Shipetiari. The reserve is divided into different land use zones, one of which is designated as a tourism and conservation area, and this was where we conducted our research. Within this survey area (approximately 252ha), a small lodge had been built and the forest had undergone minimum logging activities with only narrow access trails cut into the forest. Other zones within Shipetiari land have undergone disturbance activities such as small-scale agriculture, the clearing of land for constructing houses for the community, and subsistence logging. The Shipetiari community is made up of some 120 inhabitants (of ~24 families) who practice subsistence hunting, increasingly moving away from traditional methods such as bows and arrows, to using shotguns. Few biodiversity studies have been conducted near to the community [41] and, prior to this study, no mammal species list existed for the site. There was no intention of making a standardized comparison of the mammal communities of the two sites. Instead the objective of collecting data at the second site was to test our methodology under different circumstances, where current anthropogenic pressure was higher and the intensity of prior research carried out at the site was lower.

Data collection – Camera traps

Thirty camera traps triggered by a motion detector (Model - Bushnell 119438 Natureview Cam 8mp) were deployed across 15 arboreal sampling locations: nine at the MLC and six at Shipetiari (Fig. 1). Each sampling location contained two camera traps set at two heights: a mid-canopy camera (~10m) and a high canopy camera (ranging between 18.4-33.0m, with a mean of 26.1m ±1.1). Camera traps were programmed to work continuously, 24 hours a day, and to take 1 photo followed by a 14 second video when triggered. An interval of 30s between sets of photos and videos was set and date and time were automatically stamped on videos and photos. The trees selected for camera trap placement were situated between 400m and 800m apart, and close to existing trails. Sites were chosen based on their safety to climb and the presence of a horizontal limb suitable for camera trap placement in the upper canopy. Traps were set up in mid-June 2014 and removed before the onset of the wet season at the start of October 2014. Not all camera traps worked for the entirety of the time they were in the field. Two cameras failed straight away (likely due to the batteries becoming dislodged during setup), but 21 of the 30 cameras lasted for the full duration of the survey period. The seven cameras that failed lasted on average 65.4 camera days (ranging between 3-99 days). Camera failures were generally caused by false triggers of the camera due to moving foliage within the frame, which either depleted batteries or filled up space on the memory cards.

Overall the survey resulted in a total of 1496 mid canopy trap days and 1433 high canopy trap days (2929 total trap days, which was more than the 1000-2000 needed to accumulate 60-70% of tropical terrestrial community species richness, as suggested by Rovero et al. [42]). Of these, 885 mid canopy trap days and 896 high canopy trap days came from the MLC and 611 mid canopy trap days and 537 high canopy trap days from Shipetiari. When considered independently for different strata and across sites, effort is lower than the suggested minimum 1000 days for terrestrial communities and our results should be considered with this factor in mind. Setting up and taking down the cameras from both sites took a team of three people 21 days (12 at the MLC and nine at Shipetiari), equating to ~504 working hours (based on an eight hour working day).

Data collection: traditional methods; transects and incidental observations

Between the 15th of January 2014 and 27th of December 2014, thirty-nine timed morning transects (0530-0800) were performed across 11 different 2km transects at the MLC (~78km of timed transect walked in total). Survey teams consisted of two trained observers. Each transect was walked on three to five occasions and took an average of 128 minutes (sd = 25 mins). In total, these transect surveys represented 166 observer hours. In addition to the timed morning transects, all incidental mammal observations made whilst performing an array of other surveys (nocturnal and diurnal), were recorded. Whilst it is difficult to quantify the effort from incidental records, permanently employed MLC research staff worked extensively in the forest, day and night, all year round. Nocturnal transect and incidental data was also gathered from the MLC during the dry season of 2013 (between the 18th of March and 20th of August). This represented 249 nocturnal transect observer hours carried out along the same trail system as the diurnal surveys in 2014 (~132km of timed nocturnal transects walked in total).

Between the 13th and 30th of November 2014 a rapid biological survey expedition visited the Shipetiari region. Pairs of trained observers performed ten timed morning transects (0530-0810) across four

2km transects (~20km of timed transect walked in total), totaling 57 hours of observer effort. Incidental arboreal mammal records included observations recorded outside of the survey periods. In addition, 48 hours of survey effort (between the 12th and 26th July 2014) was carried out by an experienced primatologist and an assistant, searching morning and afternoon, specifically for woolly monkeys but recording all other arboreal mammal species too.

All transects were established on existing trails at both survey sites. Data collection dates were more varied for transects and incidental recordings with some data being collected closer to the wet season, when sites in the Western Amazon have been shown to harbor higher species richness [41]. As such, we view this as a conservative test of arboreal camera traps for rapid species inventories, with traps only deployed during a three month period during the dry season. The risk of camera trap breakages and reduced sensitivity as a result of persistent rain and humidity is less likely during the drier season [43]. In addition to this, other research suggests that, for some mammal species, seasonality affects are not significant [44]. In order to check this for our study, we reviewed the research database from the MLC (containing data between 2011 and 2015). This showed that 17 of the 22 species (77%) detected at the site are recorded year round in both wet and dry seasons (see Appendix 1). These differences should not, therefore, significantly affect the ability to detect the majority of species within this study.

Analysis

We compared arboreal medium-large mammal inventories obtained by classical ground-based approaches with inventories by arboreal camera traps in order to determine the potential of arboreal camera traps to record species that are difficult to detect. To do this we compiled data of arboreal mammals from diurnal transects at each site, from nocturnal transects (only from the MLC study site), from incidental observations and from arboreal camera traps in 2014. Camera trap detections were designated as separate events if there was at least a 30-minute interval between captures of the same species [45]. The percentage of species detected by each methodology was calculated for the MLC site against the long term ten-year species list for the site, and for the Shipetiari site against the total number of species recorded at the site in 2014 (comprising of detections from all methodologies used). The number of species which were uniquely detected by each survey methodology was also determined. In order to assess and control for differences in sampling effort, species accumulation curves were calculated using Estimates S software [46] and plotted using R [47]. Curves were produced for camera trap data from the MLC, camera trap data from Shipetiari and for pooled transect and incidental data from the MLC (it was deemed that records were too low to do this for transect data alone and from the rapid transect data at Shipetiari). The curves from camera traps were projected forwards and the combined incidental and transect data was clipped to produce comparable accumulations despite differences in sampling efforts.

The overall cost and effort for classical ground-based approaches and arboreal camera traps were compared by calculating the financial costs involved in terms of training, equipment and field site costs in relation to the person hours required to provide an equivalent number of detections for each survey methodology (diurnal transects, nocturnal transects and arboreal camera traps – based upon information from the MLC study site, which had the more intensive survey effort). Using the same methodology we also calculated cost per detection for each species detected. It should be noted that there were different detection costs for different sites due to factors such as hunting, logging intensity and level of wildlife protection.

In order to determine if there was any difference in detection frequency of arboreal mammals between mid and upper-canopy camera traps, we implemented a linear mixed effects model with a normal error structure using the 'lme4' package within the R statistical environment [47]. We used tree ID as a random effect in order to account for the non-independence of cameras within the same tree. The significance of camera trap height was assessed using a likelihood ratio test. We also indicate the potential temporal coverage per day and detection biases related to traditional transect surveys compared with arboreal camera traps. Daily patterns in detection frequency between traditional survey methods and arboreal cameras were assessed through the production of activity pattern charts using the package 'activity' within the R statistical environment [47]. We then used a Wald test to determine if the two activity profiles were significantly different to each other in the R package 'activity', with 1000 bootstrap repetitions [47]. To test whether detections per day changed in response to the length of time since the camera traps were deployed over the first four weeks a glm was used with a poisson link and day as a continuous variable. Linear mixed effects models with binomial distribution using glmm in the lme4 R package were then used to investigate whether the number of days since setting up a camera trap influenced detection probability during each 24 hour period of the first seven days. Detection was classed as 0 or 1 depending on whether a mammal was detected at each camera on each of the first seven days. Day of detection was treated as a fixed factor and models compared whether the first day, the first two days or all seven days differed in detection probability. Finally, observations of special interest were highlighted in order to assess the potential of arboreal camera traps for obtaining useful or novel ecological information.

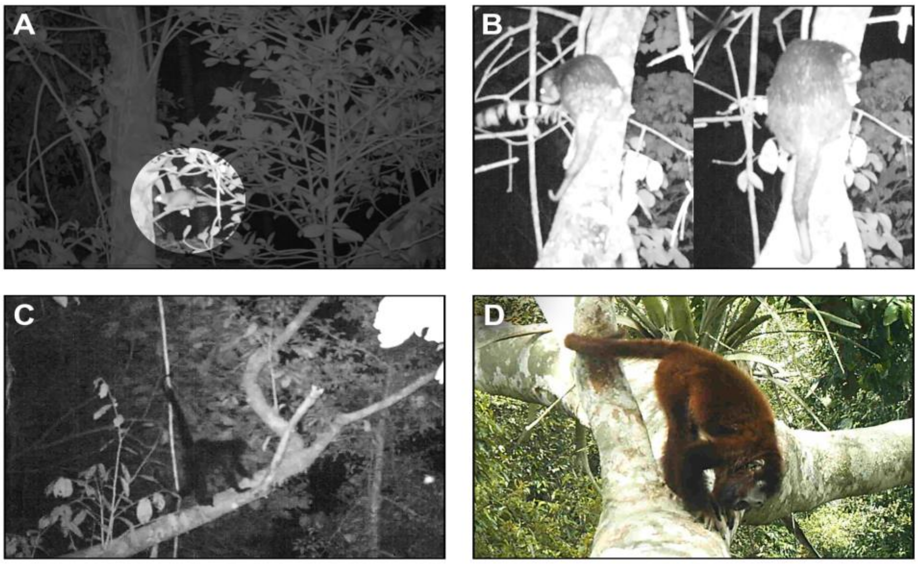

Fig. 2. A) silky pygmy anteater from the MLC, the first detection for the reserve in over 10 years of biodiversity research at the site; B) a pair of bicolour-spined porcupines from the MLC, both detected in the same tree, as observed in related species [48]; C) first record of nocturnal activity of the endangered black-faced spider monkey, detected at the MLC and D) Bolivian red howler monkey attempting to call but making no sound from Shipetiari, suggesting potential human avoidance behaviour due to hunting at the site [21, 23].

Results

Overall we detected 24 arboreal mammal species, based on 1201 separate records, 339 of which were from arboreal camera traps. In total 18 species of arboreal mammal were detected by arboreal camera traps, seven species by diurnal line transects, six species by nocturnal transects and 18 species were detected incidentally (Appendix 2; see Appendix 3 for number of detections per species). At the MLC this represented 15, four, six and 16 species for each methodology respectively. At the Shipetiari site this represented 12, six and eight species, for camera traps, diurnal transects and incidental records respectively. In addition to the 339 records we positively identified from camera traps, 34 records (9%) could not be identified. This was because sometimes only part of the animal appeared in frame, or the animal was moving too quickly out of frame, or it was hidden behind dense foliage. Of these, 13 were confirmed to be opossums but the species could not be verified, three were small mammals (rodents) and 18 were unidentifiable.

Overall, six species were identified only by camera traps. Whereas arboreal camera trapping resulted in the detection of four unique species at the MLC and six unique species at Shipetiari, no unique species were detected using diurnal visual encounter surveys (Appendix 2). Incidental records provided five unique species detections at the MLC and a single species from Shipetiari (Appendix 2). Nocturnal transects added one unique species detection at the MLC (Appendix 2). Comparison with the full MLC species list suggests that several species known to be present in the area were not detected by the arboreal cameras: Bolivian bamboo rat, brown titi monkey, margay, short-furred woolly mouse opossum and southern Amazonian red squirrel. However, arboreal camera trapping resulted in the addition of the silky pygmy anteater to the species list (Fig. 2) which had not been seen at the MLC before despite ten years of surveying using traditional survey methods.

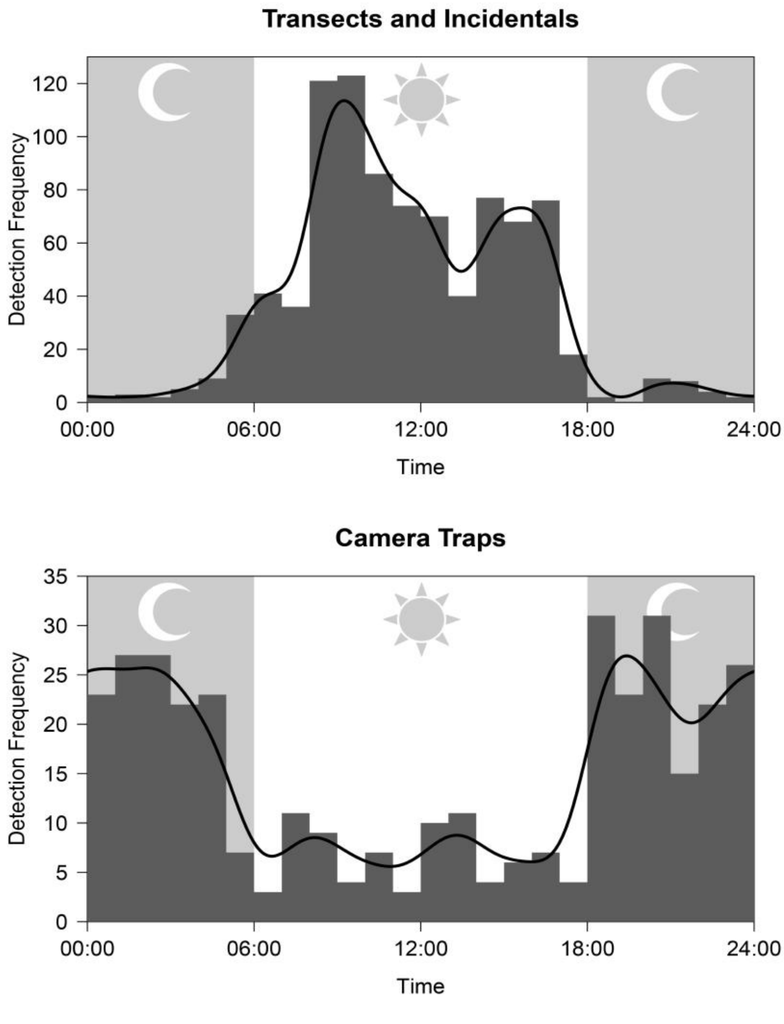

Fig. 3. Daily average detection frequency patterns of arboreal rainforest mammals using transects and incidental data from the MLC, compared with data gathered from arboreal camera traps. The histogram denotes raw detection frequency and the black line denotes the fitted spline. The Wald test used to assess statistically the two activity profiles showed that the patterns were significantly different (W=29.5, p=<0.0001).

The species accumulation curves (Appendix 4) show that the observed number of records for camera traps at both sites did not reach a plateau, and so may need more camera trap days than indicated by terrestrial based studies [42]. Despite pooling both transect and incidental data, the species accumulation curve for traditional methodologies still failed to plateau, suggesting that a greater survey effort is required to detect all species. The curves also show that cameras were able to detect a greater number of species in a lower number of initial detections but suggest that incidental and transects may detect more species as records accumulate.

Daily patterns in detection frequency were found to be strikingly different between data gathered from arboreal cameras and data gathered from traditional transects and incidental records (Fig. 3). The Wald test used to assess statistically the two activity profiles showed that the patterns were significantly different (W=29.5, p=<0.0001). Data gathered incidentally and through both diurnal and nocturnal transect surveys displayed more observations of diurnal species, whereas camera traps displayed a greater frequency of detections nocturnally than diurnally. Across the first four weeks (see Fig. 4) there was no significant effect (p=0.72) of number of days since camera trap deployment on number of detections, suggesting the process of deploying the cameras caused little long term disturbance. However Fig. 4 shows no detections occurred in the first 24 hours of deployment and this was supported by a GLMM analysis of whether a camera detected any mammals on each of the first seven days. This showed that the best fitting model (and the only one better than the null model) was one where detection rate in the first 24 hours was lower than detection rates over the following six days (Delta AIC compared to null -3.93).

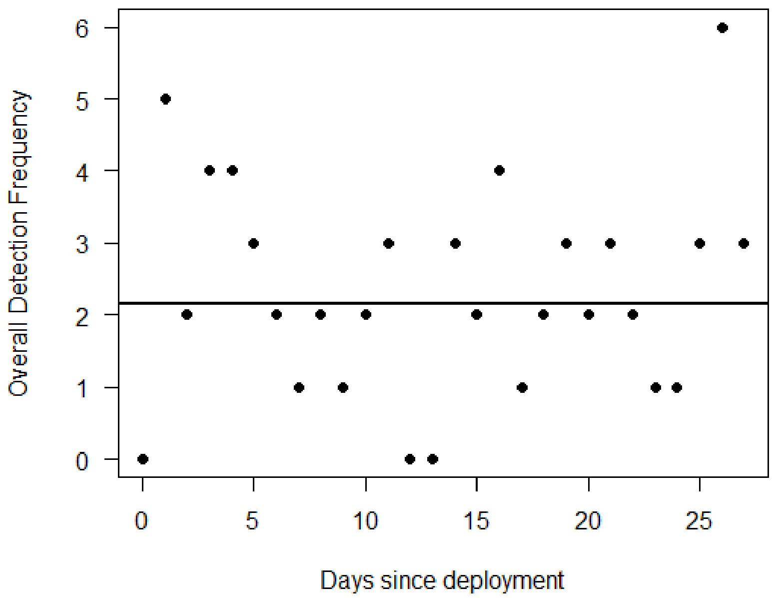

Fig. 4. Detection frequency of camera trapping in first 4 weeks since deployment, showing no consistent change over time.

Upper canopy camera traps were found to result in significantly more mammal detections than those placed in the mid-canopy (p=0.008). On average, upper-canopy traps were predicted to result in 21 mammal detections per 100 days, whereas mid-canopy traps resulted in just 0.7 detections per 100 days (see Appendix 5 for complete species detections by vertically stratified camera location). Only six arboreal mammal species were detected on mid-canopy camera traps, while 18 species were detected on upper canopy cameras. All of the species recorded on mid canopy traps were also recorded in the upper canopy, and in all but one case (the saddleback tamarin) species were detected in higher frequencies in the upper canopy (Appendix 5). Tree ID accounted for none of the variance in arboreal mammal detection frequency.

The cost effort analysis indicated that upfront costs in terms of training and equipment for arboreal camera trapping were greater than those for traditional transect surveys (Appendix 6; $10,667 versus $1178). However, when considering the total expense necessary to cover field station costs related to the person hours needed to provide equivalent numbers of observations (note: not an equivalent number of species), the overall costs balanced out considerably ($1913 to gather equivalent diurnal data plus $8499 to gather equivalent nocturnal data; $10,412 in comparison to a total of $11,757 for arboreal camera trapping which collected data both diurnally and nocturnally). Data sorting and organization was carried out for both methodologies during the field work so although there may have been some additional associated costs with data checking these would likely be equivalent for both survey methodologies.

When assessing the costs per detection for each species detected by different methods, camera traps provided financial advantages for some species, but not for others (Appendix 1 and Appendix 3). When considering nocturnal cryptic species (e.g. kinkajou, night monkey and arboreal porcupine) and some hunted primates (e.g. woolly monkey and spider monkey), the cost per detection was cheaper than transects. However, for the majority of diurnal species, particularly those which are not hunted (e.g. capuchins, squirrel monkeys, titi monkeys and tamarins), then diurnal transects were more cost-effective. When comparing arboreal cameras with nocturnal transects, camera traps detected six unique species and transects two unique species. Cameras were found to be more cost-effective for all five species detected by both methods. Arboreal camera traps detected three unique species and diurnal transects just one unique species. However, cameras were found to be more cost-effective for just one of the six species detected by both methods, diurnal transects being more cost-effective for the remaining five.

Discussion

Our results suggest that arboreal camera traps can be an effective tool for inventorying secretive rainforest mammal communities within the canopy. Cameras detected a greater number of species than either diurnal or nocturnal transects; only incidental records provided greater numbers of detections and detected a comparable number of unique species. Arboreal traps also detected a higher number of secretive rainforest mammal species than more traditional methodologies. Whilst traditional techniques tend to focus on subsets of the overall mammal community (diurnal or nocturnal), arboreal camera traps allowed for 24 hour detection of species. It is worth noting, however, that camera traps did not detect all species: some species were only recorded incidentally or along transects. Therefore, if the aim is to detect all arboreal species, a combination of traditional methodologies and the use of arboreal cameras may provide the most complete representation of arboreal mammal communities, a finding which concurs with a similar comparative study undertaken at the terrestrial level by Munari et al. [20].

Arboreal camera traps were particularly useful in the detection of active, larger-bodied, hunted species of high conservation concern [12], such as the endangered black-faced spider monkey and the Peruvian woolly monkey, but also in detecting lesser-known, cryptic species, such as the bicolour-spined porcupine [48-50] and the silky pygmy anteater [51] (Fig.2). Although such cryptic species have been recorded from a number of locations throughout Amazonia, detailed information about the ecology and distribution of both species is currently limited [49-51]. Biologists have been carrying out biodiversity surveys at the MLC since 2004, as have expedition groups and, since 2010, an all-year round field team has been dedicated to surveying the biodiversity of the reserve both day and night [40]. Despite ten years of on-going research and assessment, the nocturnal and inconspicuous, silky pygmy anteater [51, 20] had evaded detection [40]. However, in just three months, cameras at the MLC captured two separate records of this elusive species from two trees (>400m apart; Fig. 2). This provided a clear demonstration of the ability of arboreal cameras to collect novel distribution and ecological data, especially for species where this has proven difficult or impossible using traditional survey techniques.

A further potentially effective use of arboreal camera traps identified within this study is the ability of cameras to detect species in areas where hunting occurs. Mammals are often difficult to detect using traditional methodologies in hunted areas due to the human avoidance behaviors they have adopted [21,23]. For example, at Shipetiari, where hunting for subsistence is common, spider monkeys, woolly monkeys and howler monkeys had not been recorded despite extensive searches by research groups visiting the same area of the site in 2014. However, the cameras in this study detected both howler and spider monkeys within 1.5km of the community (Fig. 2).

Comparison of detection frequency and species richness between upper and mid canopy cameras suggests that upper canopy traps were more effective for rapid species inventorying than those placed lower down, with upper canopy traps accruing thirty times more detections than those placed in the mid canopy. Rather than this reflecting greater use of the upper canopy in comparison to the mid-canopy, this may have been because high trap locations were selected primarily because of the presence of large horizontal limbs whilst mid traps were placed at ~10m in height regardless of whether or not it was facing a horizontal limb. We would therefore recommend that future research look at whether locating mid-canopy traps facing large horizontal limbs might be a way of increasing species detections in the mid-canopy. Although we showed that the species inventories collected by arboreal camera trapping in the dry season alone were comparable to those obtained by year-round traditional methodologies, arboreal cameras should also be tested to determine their effectiveness during both wet and dry seasons. This is of particular importance for studies aiming to develop density estimates, which are subject to seasonal variation in arboreal mammal activity.

Despite the potential benefits in utilizing arboreal camera traps to survey arboreal rainforest mammals [39] there are, as with any method, a number of potential limitations and advantages in favor of traditional ground-based survey techniques. Direct observations, for example, may be more effective at identifying the number of individuals within a group and they could also facilitate the use of distance-sampling techniques to calculate density estimates [22]. Under the right circumstances animals can also be followed to gather detailed behavioral information on movement patterns, competition, feeding behaviors and hunting-induced behavioral changes [23,52]. However, arboreal camera trapping remains in its infancy as a survey and monitoring technique and, as with terrestrial based camera traps, there is the potential to further develop analysis techniques and sampling regimes that can provide density estimates [e.g. 28-33,53] and, in so doing, gather more detailed ecological information about elusive arboreal mammals [38,39,54].

Arboreal camera trapping might initially seem unattractive to money-constrained conservation scientists due to the large capital investment required for training and equipment [55,56]. However, cost estimates here refer to a single field season of data collection and since training is typically a one-off investment (unless further skills are being developed or technique refreshment is needed) and equipment can be re-used in future assessments (only needing re-investment due to wear and tear or breakages), costs divided over multiple field seasons are potentially lower. As traditional survey methods require longer field stays in order to provide equivalent size data sets for some species, the costs of using traditional techniques are often likely to outweigh the larger initial investment required for arboreal camera surveys in the long-term but, as stated above, there may be additional costs for equipment maintenance and replacement, which are unaccounted for in the financial assessment of the field season within this study.

From our assessment of the associated costs per detection for each species, we present three general recommendations for researchers looking to study arboreal mammals: i) if the target group is made up of diurnal species, in the absence of hunting, then diurnal transects and incidental recordings are likely to be the most cost-effective methodology; ii) if the target species are secretive, nocturnal or hunted species, then camera traps may be the preferable and most cost-effective choice; iii) if the aim of the survey is to detect the complete arboreal mammal community, then a combination of the above survey methods may be best (as previously shown with terrestrial methodologies [20]). Further research seeking to determine whether the suggestions from this initial work are applicable to other regions and contexts is recommended.

Implications for conservation

In a rapidly changing era, currently acknowledged by many as the anthropocene, where the condition of the world's tropical forests is being modified at an alarming rate [57], rapid and cost effective survey techniques can provide invaluable tools for understanding how tropical fauna are responding to such changes. This can consequently facilitate increased awareness about the biodiversity and conservation value of both primary and regenerating tropical forests [58]. Understanding the effects of anthropogenic disturbance to canopy environments is particularly important given that a number of different taxonomic assessments have suggested that biodiversity within canopy strata is under greatest threat due to habitat modification [4,7-11,59]. Here we suggest that the arboreal camera trapping method can be both useful and cost-effective in the long term for conservation assessments and can provide opportunities to learn more about some of the most charismatic [12] and threatened species in the world [38,39,54] which may otherwise remain largely unknown and could quietly disappear from our planet.

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Appendix 1 – Overall species detections and associated costs per detection for each methodology. Where: ACT = Arboreal Camera Trapping, DT = Diurnal Transects; NT = Nocturnal Transects.

Common name	Species name	Total study detections	Overall cost per detection for this study			Present year round?
			ACT	DT	NT	
Allen's olingo	*Bassaricyon alleni*	1	$11,757			
Bicolour-spined porcupine	*Coendou bicolor*	8	$1,960		$2,449	
Black-eared common opossum	*Didelphis marsupialis*	2	$5,879			✓
Black-faced spider monkey	*Ateles chamek*	57	$2,125			✓
Bolivian bamboo rat	*Dactylomys boliviensis*	1			$,2449	
Bolivian red howler monkey	*Alouatta sara*	66	$1,960	$857		✓
Bolivian squirrel monkey	*Saimiri boliviensis*	173	$1,176	$857		✓
Brown titi monkey	*Callicebus brunneus*	186		$122		✓
Brown-eared woolly opossum	*Caluromys lanatus*	43	$273			
Four-eyed opossums (Brown/Gray)	*Metachirus nudicaudatus / Philander opossum*	18	$653			✓
Gray monk saki monkey	*Pithecia irrorata*	2	$5,879			
Hoffman's two-toed sloth	*Choloepus hoffmanni*	5	$3,919		$2,449	✓
Kinkajou	*Potos flavus*	67	$210		$408	✓
Large-headed capuchin	*Sapajus macrocephalus*	192	$840	$643		✓
Margay	*Leopardus wiedii*	1				✓
Peruvian night monkey	*Aotus nigriceps*	167	$90		$306	✓
Peruvian woolly monkey	*Lagothrix cana*	132	$392	$1285		✓
Saddleback tamarin	*Saguinus fuscicollis*	56	$2,351	$1285		✓
Short-furred woolly mouse opossum	*Micoureus regina*	3			$1225	✓
Silky pygmy anteater	*Cyclopes didactylus*	2	$5,879			
Southern Amazonian red squirrel	*Sciurus spadiceus*	8		$2570		✓
Tamandua	*Tamandua tetradactyla*	5	$5,879			✓
White-fronted capuchin	*Cebus albifrons*	5	$2,939			
White-bellied slender mouse opossum	*Marmosops noctivagus*	1				✓

Appendix 2 – Comparison of arboreal mammal species inventories using camera traps and traditional survey techniques. Where IUCN RL = IUCN Red List; LC = Least Concern; NT = Near Threatened; E = Endangered; D = Decreasing; S = Stable; U = Unknown; ACT = Arboreal Camera Traps; DT = Diurnal transects; NT = Nocturnal Transects; and INC = Incidentals.

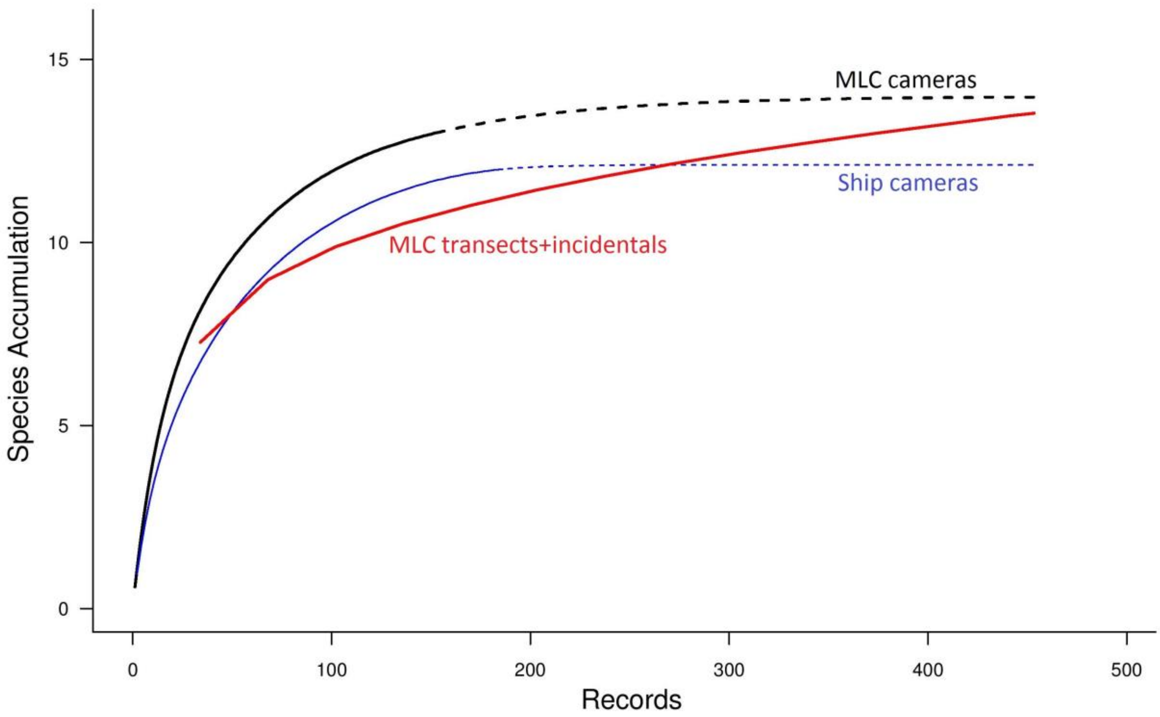
Common name	Species name	IUCN RL status	IUCN population trend	Diurnal or Nocturnal	Manu Learning Centre					Shipetiari N. C.			
					Ten year species list	ACT	DT	NT	INC	Total from 2014	ACT	DT	INC
Allen's olingo	*Bassaricyon alleni*	LC	D	N	✓	✓							
Bicolour-spined porcupine	*Coendou bicolor*	LC	U	N	✓	✓		✓	✓				
Black-eared common oppossum	*Didelphis marsupialis*	LC	S	N	✓					✓	✓		
Black-faced spider monkey	*Ateles chamek*	E	D	D	✓	✓			✓	✓	✓		
Bolivian bamboo rat	*Dactylomys boliviensis*	LC	S	N	✓			✓		✓			✓
Bolivian red howler monkey	*Alouatta sara*	LC	D	D	✓	✓	✓		✓	✓	✓	✓	
Bolivian squirrel monkey	*Saimiri boliviensis*	LC	D	D	✓	✓			✓	✓	✓	✓	✓
Brown titi monkey	*Callicebus brunneus*	LC	U	D	✓		✓		✓	✓		✓	✓
Brown-eared woolly opossum	*Caluromys lanatus*	LC	D	N	✓	✓				✓	✓		
Four-eyed opossums (Brown/Gray)	*Metachirus nudicaudatus / Philander opossum*	LC	S	N	✓	✓							
Gray monk saki monkey	*Pithecia irrorata*	-	-	D						✓	✓		
Hoffman's two-toed sloth	*Choloepus hoffmanni*	LC	U	N	✓	✓		✓	✓				
Kinkajou	*Potos flavus*	LC	D	N	✓	✓		✓	✓	✓	✓		
Large-headed capuchin	*Sapajus macrocephalus*	LC	D	D	✓	✓	✓		✓	✓	✓	✓	✓
Margay	*Leopardus wiedii*	NT	D	N/D	✓				✓				
Peruvian night monkey	*Aotus nigriceps*	LC	U	N	✓	✓		✓	✓	✓	✓		✓
Peruvian woolly monkey	*Lagothrix cana*	E	D	D	✓	✓	✓		✓				
Saddleback tamarin	*Saguinus fuscicollis*	LC	D	D	✓				✓	✓	✓	✓	✓
Short-furred woolly mouse oppossum	*Micoureus regina*	LC	S	N	✓			✓	✓				
Silky pygmy anteater	*Cyclopes didactylus*	LC	U	N	✓	✓							
Southern Amazonian red squirrel	*Sciurus spadiceus*	LC	U	D	✓				✓	✓		✓	✓
Southern tamandua	*Tamandua tetradactyla*	LC	U	N/D	✓				✓	✓	✓		
White-fronted capuchin	*Cebus albifrons*	LC	D	D						✓	✓		✓

White-bellied slender mouse opossum	*Marmosops noctivagus*	LC	S	N	✓				✓				
Observed species					22	13	4	6	16	15	12	6	8
% detected of total list						59	18	27	73		80	40	53
Unique species detected						4	0	1	5		6	0	1
Person working hours in the forest						288	166	249	na		216	105	Na

Appendix 3 – Site-specific species detections and associated costs per detection for each methodology, across the two study sites. Where: ST = Site Total (total number of observations across all methodologies), CPD = Cost Per Detection, ACT = Arboreal Camera Trapping, DT = Diurnal Transects; NT = Nocturnal Transects; INC = Incidentals.

Common name	Species name	Manu Learning Centre								Shipetiari N. C.					
		ST	ACT	CPD	DT	CPD	NT	CPD	INC	ST	ACT	CPD	DT	CPD	INC
Allen's olingo	*Bassaricyon alleni*	1	1	$5,676						0					
Bicolour-spined porcupine	*Coendou bicolor*	8	6	$946			1	$2,449	1	0					
Black-eared common oposum	*Didelphis marsupialis*	0								2	2	$2,027			
Black-faced spider monkey	*Ateles chamek*	56	3	$1,892					53	1	1	$4,054			
Bolivian bamboo rat	*Dactylomys boliviensis*	1					1	$2,449		0					
Bolivian red howler monkey	*Alouatta sara*	61	3	$1,892	1	$1,564			57	5	3	$1,351	2	$503	
Bolivian squirrel monkey	*Saimiri boliviensis*	160	4	$1,419					156	13	6	$676	3	$335	4
Brown titi monkey	*Callicebus brunneus*	171			12	$130			159	15			9	$112	6
Brown-eared woolly oposum	*Caluromys lanatus*	41	41	$138						2	2	$2,027			
Four-eyed opossums (Brown/Gray)	*Metachirus nudicaudatus / Philander opossum*	18	18	$315						0					
Gray monk saki monkey	*Pithecia irrorata*	0								2	2	$2,027			
Hoffman's two-toed sloth	*Choloepus hoffmanni*	5	3	$1,892			1	$2,449	1	0					
Kinkajou	*Potos flavus*	29	18	$315			6	$408	5	38	38	$107			
Large-headed capuchin	*Sapajus macrocephalus*	177	2	$2,838	3	$521			172	15	12	$338	1	$1,005	2
Margay	*Leopardus wiedii*	1							1	0					
Peruvian night monkey	*Aotus nigriceps*	55	22	$258			8	$306	25	112	109	$37			3
Peruvian woolly monkey	*Lagothrix cana*	132	30	$189	2	$782			100	0					
Saddleback tamarin	*Saguinus fuscicollis*	44							44	12	5	$811	2	$503	5
Short-furred woolly mouse opossum	*Micoureus regina*	3					2	$1,224	1	0					
Silky pygmy anteater	*Cyclopes didactylus*	2	2	$2,838						0					
Southern Amazonian red squirrel	*Sciurus spadiceus*	5							5	3			1	$1,005	2
Tamandua	*Tamandua tetradactyla*	3							3	2	2	$2,027			
White-fronted capuchin	*Cebus albifrons*	0								5	4	$1,014			1
White-bellied slender mouse opossum	*Marmosops noctivagus*	1							1	0					

Appendix 4 – Accumulation curves for arboreal camera traps at the MLC (black line), camera traps at Shipetiari (blue line) and on pooled data from both incidental and transect based data from the MLC (red line). Solid lines represent observed records and dashed lines represent a projection using EstimateS [46].



Appendix 5 - Total identifiable arboreal vertebrate detections stratified by vertical camera location.

Common name	Species name	Mid-canopy			Upper-canopy		
		Observed	Frequency / 100 trap nights	Frequency / camera	Observed	Frequency / 100 trap nights	Frequency / camera
Allen's olingo	*Bassaricyon alleni*	0	0	NA	1	0.07	0.07
Bicolour-spined porcupine	*Coendou bicolor*	0	0	NA	6	0.42	0.07
Black-banded woodcreeper	*Dendrocolaptes picumnus*	0	0	NA	1	0.07	0.07
Black-eared common oppossum	*Didelphis marsupialis*	0	0	NA	2	0.14	0.07
Black-faced spider monkey	*Ateles chamek*	0	0	NA	4	0.28	0.21
Bolivian red howler monkey	*Alouatta sara*	0	0	NA	6	0.42	0.21
Bolivian squirrel monkey	*Saimiri boliviensis*	2	0.13	0.14	8	0.56	0.29
Brown-eared woolly opossum	*Caluromys lanatus*	0	0	NA	43	3	0.29
Double-toothed kite	*Harpagus bidentatus*	0	0	NA	1	0.07	0.07
Four-eyed opossums (Brown/Gray)	*Metachirus nudicaudatus / Philander opossum*	0	0	NA	18	1.26	0.07
Gray monk saki monkey	*Pithecia irrorata*	0	0	NA	2	0.14	0.07
Hoffman's two-toed sloth	*Choloepus hoffmanni*	0	0	NA	3	0.21	0.07
Kinkajou	*Potos flavus*	2	0.13	0.14	54	3.77	0.71
Large-headed capuchin	*Sapajus macrocephalus*	1	0.07	0.07	13	0.91	0.21
Olive oropendola	*Psarocolius bifasciatus*	1	0.07	0.07	5	0.35	0.29
Pale-winged trumpeter	*Psophia leucoptera*	0	0	NA	1	0.07	0.07
Paradise tanager	*Tangara chilensis*	0	0	NA	1	0.07	0.07
Peruvian night monkey	*Aotus nigriceps*	0	0	NA	131	9.14	0.64
Peruvian woolly monkey	*Lagothrix cana*	3	0.2	0.07	27	1.88	0.21
Razor-billed curassow	*Mitu tuberosum*	0	0	NA	1	0.07	0.07

Russte-backed oropendola	*Psarocolius angustifrons*	0	0	NA	1	0.07	0.07
Saddleback tamarin	*Saguinus fuscicollis*	3	0.2	0.07	2	0.14	0.07
Silky pygmy anteater	*Cyclopes didactylus*	0	0	NA	2	0.14	0.14
Spix's guan	*Penelope jacquacu*	0	0	NA	9	0.63	0.36
Tamandua	*Tamandua tetradactyla*	0	0	NA	2	0.14	0.14
Unidentified nightjar	NA	0	0	NA	1	0.07	0.07
Unidentified woodcreeper	NA	0	0	NA	3	0.21	0.14
Violaceus jay	*Cyanocorax violaceus*	0	0	NA	1	0.07	0.07
White hawk	*Pseudastur albicollis*	0	0	NA	2	0.14	0.07
White-fronted capuchin	*Cebus albifrons*	1	0.07	0.07	3	0.21	0.07
Observed mammal species richness			**6**			**18**	
Observed total species richness			**7**			**30**	

Appendix 6 – Overall cost-effort analysis of arboreal camera trapping versus traditional transect techniques for the field season within this study. Note: this relates to the effort required to gather an equivalent number of observations, not an equivalent number of species. Cost per detection for each species (where detected) are provided in Appendices 1 and 3.

Method	Line transect	Camera traps
Number of detections / 100 person field-work hours	8 nocturnal 22 diurnal	77 nocturnal 22 diurnal
Daily Coverage	6hrs of survey effort per day possible for researchers	24hrs
Estimated field station days needed to gather equivalent number of observations (to camera trapping in this study)	121 nocturnal 12 diurnal	12
Training costs and additional insurance cover (USD)	Training period for seven days; research station fee for two researchers $424	BCAP Climbing course: $1080 additional insurance cover for climbing activities: $300 = $1380 total
Equipment costs (USD)	Recording equipment, microphone, head torch. $754 total	Climbing equipment: $2027 Camera traps / unit: $242 (x30 units for this study) = $7261 total
Data sorting and validation	Mostly carried out on site but may need some further verification post-trip (1-2 days)	Mostly carried out on site but may need some further verification post-trip (1-2 days)
Total field station costs - to gather an equivalent number of observations (USD)	$7321 nocturnal (2 people for 121 days @$30.25/day) $735 diurnal (2 people for 12 days @$30.25/day)	$1089 (3 people for 12 days @$30.25/day)
Total projected cost; field station costs + training + equipment - to gather equivalent number of observations (USD)	$8499 nocturnal $1913 diurnal **$10,412 overall**	**$11,757 overall**